

Diagnoses of hybrid hummingbirds (Aves: Trochilidae).
13. An undescribed intrageneric combination,
Heliodoxa imperatrix* × *Heliodoxa jacula

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Abstract.—An enigmatic specimen collected by Perry O. Simons, presumably on the Pacific slope of the Ecuadorian Andes, is demonstrated to be a hybrid between *Heliodoxa imperatrix* and *Heliodoxa jacula jamesoni*. This represents the only known instance of intrageneric hybridization in *Heliodoxa*. External measurements of the hybrid are consistent with the proposed parental hypothesis.

At the monthly meeting of the British Ornithologists' Club on the 17 January 1900, Ernst Hartert (1900:39) exhibited a specimen of hummingbird, "obtained in Ecuador by Mr. Simons, combin[ing] in a striking way the shape and colours of *Eugenia [Heliodoxa] imperatrix* and *Heliodoxa jacula jamesoni* . . . to be described in detail in the 'Novitates Zoologicae'." Although Hartert never published a description or reported a museum registration number, this brief exhibition notice has been cited in catalogs of avian hybrids (Gray 1956, Panov 1989). Here I provide a taxonomic assessment of the specimen employing the methods and assumptions outlined in Graves (1990) and Graves & Zusi (1990), as modified by the findings of Graves (1998, 1999).

Methods

The specimen, now deposited in the Natural History Museum (registration number, 1902.3.13.2211), bears two labels, one from the British Museum marked "P. O. Simons," and an older one from the Rothschild Museum. Perry O. Simons collected mammals and birds for Oldfield Thomas (British Museum) from 1898 until his murder near Cuervas, Argentina, in 1901 (Allen 1903, Chubb 1919). Both specimen labels

are marked with Hartert's taxonomic determination. Curiously, neither the specimen labels nor the Natural History Museum catalog indicate when or where the specimen was collected.

I compared the specimen (Figs. 1, 2) with all species in the subfamily Trochilinae, the typical hummingbirds (Zusi & Bentz 1982, Sibley & Monroe 1990, Bleweiss et al. 1997), deposited in the Natural History Museum, Tring, and the National Museum of Natural History, Smithsonian Institution. The specimen appears to be a male in definitive plumage as judged by the absence of striations on the maxillary ramphotheca and the presence of a well-defined, strongly iridescent gorget and coronal stripe. Descriptions in this paper refer to definitive male plumage. Simons' specimen is clearly assignable to the genus *Heliodoxa* in possessing a unique combination of characters: (a) robust, moderately long (22.7 mm), nearly straight bill (Fig. 1); (b) feathers extend forward on the bill obscuring the nostrils; (c) unmodified regimens; (d) tarsal feathers extend to the base of toes; (e) moderately forked tail (fork depth = 35.3 mm; Fig. 2), (f) unspotted rectrices; (g) small brilliant gorget; and (h) brilliant coronal stripe.



Fig. 1. A probable hybrid, *Heliodoxa imperatrix* × *H. jacula jamesoni* (BMNH 1902.3.13.2211).

According to Chubb (1919), Stephens & Traylor (1983), and Paynter (1993), Simons' collecting itinerary overlapped the known range of the genus *Heliodoxa* on the Pacific slope of the Ecuadorian Andes (prov. Azuay, Cañar, Chimborazo, Guayas, and El Oro), and on the Amazonian slope of the Andes in Peru (depto. Junín and Puno) and Bolivia (depto. La Paz). For the purposes of the hybrid diagnosis, I restricted the pool of potential parental species (Graves 1990, Graves & Zusi 1990) to *Heliodoxa aurescens*, *H. rubinoides*, *H. leadbeateri*, *H. schreibersii*, *H. branickii*, *H. imperatrix*, and *H. jacula jamesoni* (taxonomy

of Schuchmann 1999). I measured selected specimens with digital calipers (rounded to the nearest 0.1 mm): wing chord; bill length (from anterior extension of feathers); and rectrix length (from point to insertion of the central rectrices to the tip of each rectrix) (Table 1). Pairs of rectrices are numbered from the innermost (R1) to the outermost (R5).

I evaluated the color of the breast at the ventral midline and of the medial vane of the dorsal surface of R4 (7 mm from tip) with a calibrated colorimeter (CR-221 Chroma Meter, Minolta Corporation) equipped with a 3.0 mm aperture. The mea-

Table 1.—Ranges (mean ± standard deviation) of measurements (mm) of adult males of *Heliodoxa imperatrix*, *H. jacula jamesoni*, and a probable hybrid, *Heliodoxa imperatrix* × *H. jacula jamesoni* (BMNH 1902.3.13.2211).

	<i>Heliodoxa imperatrix</i> (n = 10)	<i>Heliodoxa jacula jamesoni</i> (n = 12)	BMNH 1902.3.13.2211
Wing chord	70.4–75.8 (73.2 ± 1.7)	73.3–79.0 (75.9 ± 1.8)	75.5
Bill length	23.3–24.9 (23.4 ± 0.8)	21.8–24.4 (23.2 ± 0.7)	22.7
Rectrix 1	22.6–26.6 (24.5 ± 1.2)	32.7–35.5 (33.7 ± 1.0)	28.7
Rectrix 2	27.9–32.9 (29.7 ± 1.4)	36.7–40.0 (38.5 ± 1.0)	34.3
Rectrix 3	38.7–46.5 (41.3 ± 2.3)	42.3–46.5 (44.4 ± 1.1)	43.7
Rectrix 4	51.0–60.3 (54.8 ± 2.8)	47.7–51.3 (49.7 ± 1.3)	55.6
Rectrix 5	62.2–76.2 (68.4 ± 5.7)	48.5–54.3 (51.7 ± 2.1)	64.0

asuring head of the CR-221 uses 45° circumferential illumination. Light from the pulsed xenon arc lamp is projected onto the specimen surface by optical fibers arranged in a circle around the measurement axis to provide diffuse, even lighting over the measuring area. Only light reflected perpendicular to the specimen surface is collected for color analysis. Colorimetric data from iridescent feathers are acutely dependent on the angle of measurement, the curvature of plumage surfaces in museum skins, and the degree of pressure applied to the plumage surface by the Chroma Meter aperture. In order to reduce measurement variation, I held the aperture flush with the surface of the breast plumage or rectrix without depressing it. The default setting for the CR-221 Chroma Meter displays mean values derived from three sequential, in situ measurements. I repeated this procedure twice, removing the aperture between trials. Thus, each datum summarized in Table 2 represents the mean of six independent colorimetric measurements.

Colorimetric characters were described in terms of opponent-color coordinates (L , a , b) (Hunter & Harold 1987). This system is based on the hypothesis that signals from the cone receptors in the human eye are coded by the brain as light-dark (L), red-green (a), and yellow-blue (b). The rationale is that a color cannot be perceived as red and green or yellow and blue at the same time. Therefore "redness" and "greenness" can be expressed as a single value a , which is coded as positive if the color is red and negative if the color is green. Likewise, "yellowness" or "blueness" is expressed by b for yellows and $-b$ for blues. The third coordinate, L , ranging from 0 to 100, describes the "lightness" of color; low values are dark, high values are light. The more light reflected from the plumage, the higher the L value will be. Visual systems in hummingbirds (e.g., Goldsmith & Goldsmith 1979) differ significantly from those of humans and the relevance of opponent color coordinates to col-

ors perceived by hummingbirds is unknown.

Results and Discussion

I considered hypotheses that the specimen represents (i) an undescribed geographic variant or genetic color morph of one of the aforementioned species of *Heliodoxa*; (ii) a hybrid; or (iii) an undescribed species of *Heliodoxa*. Simons' specimen does not appear to represent an unknown color morph or geographic variant of any described species because of its unique tail morphology (Table 1). As noted by Hartert (1900), the specimen combines characters of *Heliodoxa imperatrix* and *Heliodoxa jacula* (Figs. 1–3; Tables 1, 2).

The hybrid diagnosis focuses on the identification of apomorphic character states of possible parental species in putative hybrids (Graves 1990). Complete dominance and polygenic inheritance of plumage characters, however, may preclude or obscure the expression of parental apomorphies in hybrids. When parental apomorphies are not identifiable, the parentage of a hybrid may be indicated, although less conclusively, by the presence or absence of a suite of plesiomorphic characters.

The pool of potential parental species may first be narrowed by focusing on the absence of rufous or buff pigmentation in the hybrid's plumage. Because brown and reddish-brown pigments appear to exhibit consistent penetrance in hummingbird hybrids (Banks & Johnson 1961, Graves & Newfield 1996), *Heliodoxa rubinoides* (rufous on inner vanes of secondaries and primaries; cinnamon-buff margins of breast and abdominal feathers), *H. aurescens* (rufous pectoral band), and *H. branickii* (rufous inner vanes of rectrices) can be eliminated from further consideration as parental species. In a similar fashion, *H. schreibersi* (black throat, breast, and abdomen) and *H. leadbeateri* (brilliant violet coronal stripe; coppery-bronze hindercrown and neck) are exceedingly unlikely to be paren-

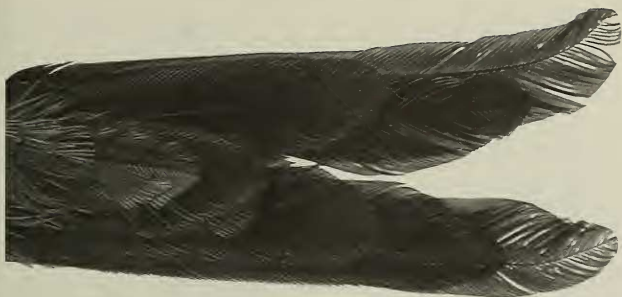


Fig. 2. Dorsal surface of the rectrices of a probable hybrid, *Heliodoxa imperatrix* \times *H. jacula jamesoni* (BMNH 1902.3.13.2211).

tal species because they possess characters not observed in the hybrid. Based on plumage characters, the hybrid is most likely the product of the species, *H. imperatrix* \times *H. jacula jamesoni*. Below, I present a synopsis of the essential evidence.

The visual display of iridescence in *Heliodoxa imperatrix* and *H. jacula* has evolved to be viewed head-on. Both parental species possess brilliant gorgets and coronal stripes that exhibit metallic iridescence. In *H. imperatrix*, the green coronal stripe is bluntly triangular in shape, extending from the base of the bill and narrowing to a point along the midline of the crown (even with the anterior edge of the eye). The bluish-green coronal stripe in *H. jacula* extends from the bill to the hindcrown forming a coronal stripe. The coronal stripe of the hybrid is intermediate in appearance between those of *H. imperatrix* and *H. jacula*. *Heliodoxa imperatrix* possesses a small purplish-pink gorget that appears to be surrounded by a field of dimly glowing, greenish-black plumage when viewed head-on. The blue gorget of *H. jacula* is surrounded by a field of green plumage, which is spangled with glowing iridescence when viewed head-on. In the hybrid, the color

and quality of iridescence exhibited by the gorget (purple exhibiting pinkish tones at certain angles) and the surrounding plumage are intermediate in appearance between those of *H. imperatrix* and *H. jacula*.

The ventral plumage of *Heliodoxa imperatrix* exhibits brilliant golden-green iridescence on the lower breast, flanks, and abdomen when viewed head-on. The breast and abdominal plumage is significantly darker in *H. jacula* and exhibits far less iridescence than in *H. imperatrix*. The color and quality of iridescence in the hybrid is intermediate between those of the postulated parental species (Table 2). The rectrices of *H. imperatrix* are dark bronzy-olive becoming progressively darker from R1 to R5, whereas those of *H. jacula* are bluish-black (the lateral webs of R1 are tinted with olive in some individuals). Rectrix color in the hybrid is roughly intermediate between that of the postulated parental species (Table 2).

As a second step, the parental hypothesis was tested with an analysis of size and external proportions (Table 1, Fig. 3). Measurements of avian hybrids fall within the mensural ranges exhibited by their parental species as a consequence of a polygenic

Table 2.—Maxima, minima, and means (\pm standard deviation) of opponent color coordinates (L , a , b) of breast and rectrix 4 (R4) for males in definitive plumage of *Heliodoxa imperatrix*, *H. jacula jamesoni*, and a hybrid, *Heliodoxa imperatrix* \times *H. jacula jamesoni* (BMNH 1902.3.13.2211).

	<i>Heliodoxa imperatrix</i> ($n = 10$)					<i>H. jacula jamesoni</i> ($n = 12$)					BMNH 1902.3.13.2211
	Min.	Max.	Mean	(\pm S.D.)		Min.	Max.	Mean	(\pm S.D.)		
Breast	L	17.3	28.8	21.4	(± 3.2)	26.5	33.5	29.3	(± 1.8)	24.4	
	a	-18.6	-8.6	-12.5	(± 3.0)	-20.1	-6.7	-13.9	(± 3.9)	-10.9	
R4	b	10.9	18.8	13.8	(± 2.7)	10.8	20.9	15.1	(± 3.4)	19.5	
	L	11.3	19.3	15.7	(± 2.3)	10.3	15.4	13.3	(± 1.7)	11.5	
	a	-1.5	2.3	0.9	(± 1.2)	0.5	2.3	1.2	(± 0.6)	2.6	
	b	4.8	11.3	7.9	(± 2.0)	-2.5	1.1	-0.8	(± 1.0)	1.6	

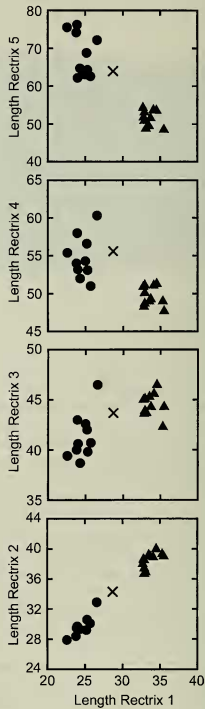


Fig. 3. Bivariate plots of measurements (see Table 1) of males in definitive plumage: *Heliodoxa imperatrix* (●), *H. jacula jamesoni* (▲), and a hybrid (X), *Heliodoxa imperatrix* \times *H. jacula jamesoni* (BMNH 1902.3.13.2211).

mode of inheritance (see Buckley 1982). Measurements of *H. imperatrix* and *H. jacula* overlap for four of seven characters. The percent difference in character means (larger species divided by smaller) varies

from negligible to moderate: wing chord (3.7%), bill length (0.9%), R1 (37.6%), R2 (29.6%), R3 (7.5%), R4 (10.3%), and R5 (32.3%). Measurements of the hybrid fall within the cumulative range of parental measurements for all seven characters and within the parental means for five characters (wing chord, R1, R2, R3, R5). In summary, evidence obtained from plumage color and pattern, as well as from external size and shape, is consistent with the hypothesis that Simons' specimen is an intrageneric hybrid between *Heliodoxa imperatrix* and *H. jacula jamesoni*.

Simons collected avian specimens on the Pacific slope of the Ecuadorian Andes in the provinces of Azuay, Chimborazo, Guayas, El Oro, and Pichincha from 1 November 1898 to 12 July 1899 (Chubb 1919, Paynter 1993). His northernmost collecting locality, Guailabamba, Pichincha (0°04'S, 78°21'W), lies in a semi-arid intermontane valley some 30 km southeast of the zone of sympatry for *Heliodoxa imperatrix* and *H. jacula jamesoni* in humid cloud forest on the Pacific slope (see Ridgely & Greenfield 2001). This suggests one of three possibilities: (1) Simons collected the specimen along the Quito-Guailabamba-Gualea road, but on the Pacific slope; (2) he purchased the specimen from a third party, possibly a native collector; or (3) he obtained the specimen at an unknown area of sympatry between the parental species on the Pacific slope in west-central or southwestern Ecuador. Whatever the source, Simons' specimen represents the only known instance of intrageneric hybridization in *Heliodoxa*.

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